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(233)*

Emergence of Chironomidae (Diptera) from continental water bodies of different climatic zones as a factor determining the food supply of fish

by Ye.V. Borutsky, Department of
Ichthyology of Moscow State University

Chironomidae play an important role in the economics of continental water bodies of all the climatic zones. Constituting, as a rule, the main part of the biomass of the benthos, they are the main food of benthophagous fishes and are utilized by them at all the stages of development. As a number of investigations has shown, the period of pupation of the larvae and ascent of the pupae is the most favourable one for the consumption of chironomids by fish; therefore, the number of emergences, their time, magnitude and duration greatly determine not only the dynamics of the larval population and biomass and the annual production of Chironomidae in a body of water, but also the food consumed in a body of water by fish [Borutsky, 1959] and the food supply of the fish.

This study is aimed at clarifying the mechanisms that govern the changes in the number of emergences and generations of Chironomidae in the waters of different climatic zones and the importance of these emergences to the food supply of the fish. Data from the

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literature and our own observations on the ecology of chironomids were used in the study. We limited ourselves only to the eurythermal species of the genus Chironomus, since these species (the largest and most valuable as a food for fish) are encountered in different types of waters throughout the world, and in most of them constitute the main nucleus of not only the Chironomidae, but often the entire benthos. In contrast to the stenothermal psychrophilic species of the genus which thrive at low temperatures, usually inhabit the profundal zone of water bodies and produce one generation a year, eurythermal species can reproduce in a wide range of temperature conditions. The prolific species that play a significant role in the biomass of the benthos and the feeding of fish include Chironomus (Ch.) plumosus L., Ch. (Ch.) behningi Goetgh., Ch. (Ch.) cingulatus Meig., Ch. (Ch.) dorsalis Meig., Ch. (Ch.) obtusidens Goetgh., Ch. (Ch.) annularius Meig., Ch. (Ch.) heterodentatus Konst., Ch. (Ch.) decorus Joh., Ch. (Camptochironomus) tentans F., etc., to which the larval forms of Chironomus f. l. plumosus, Ch. f. l. reductus, Ch. f. l. semireductus, Ch. f. l. salinarius and Ch. f. l. thummi correspond.

Number of emergences and generations in relation to the geographic location of a body of water

The number of generations of Chironomidae depends on the rate of larval development which, in turn, is related to temperature, as well as feeding conditions, respiration and other factors (Thienemann, 1954; Konstantinov, 1958, etc.). Temperature is the main factor that affects the rate of larval development. The (234) "sum-of-temperatures principle" is extensively used in entomology

to determine the possible number of generations under different temperature conditions. These sums are available for certain species of Chironomus (Mundie, 1957; Konstantinov, 1958, etc.). On the basis of these sums, we can see that only one generation a year is possible in subarctic waters. However, Teiji Kariya (1955) and A.S. Konstantinov (1958) have shown that Ch. dorsalis deposits its eggs and emerges all year round at a constant room temperature under laboratory conditions. Judging by this fact alone, it is obvious that the number of emergences and generations in waters of different climatic zones should differ.

Fig. 1 gives the results of our analysis of published data on the cyclicity of the eurythermal species of the genus Chironomus in waters of different climatic zones in the northern hemisphere between 30 and 50° E long. To eliminate the effect of the level of a body of water above the sea and its morphology, we examined only those located not higher than 200 m above sea level, shallow water bodies (up to 2 m deep), or the littoral zone of deep bodies of water (also up to 2 m deep). The climatic zonation is after V.P. Alisov et al. (1952).

The Arctic climatic zone between 30 and 50° E long. takes in only the western islands of Franz Josef Land (Alisov, 1956). There is very little information on the fauna of the inland waters of this archipelago, and hardly any information at all on the Chironomidae. In the high-arctic water bodies of this zone which are fed only by arctic waters, the temperature and trophic conditions generally prevent the development of larvae in them. An example is Lake Hazen on Ellesmere Island in arctic Canada (81°N

and 85° W) where the water temperature throughout the year does not exceed 3° (McLaren, 1961) (Fig. 1, A), or the lakes of the Banger oasis in the antarctic climatic zone (66° S and 100°E) which, according to V.S. Korotkevich (1958) contain no chironomid larvae. I.I. Greze (1953) has some data on the biology of chironomids from the arctic waters of more southern latitudes, but other longitudes, for Lake Taimyr (74-75° N and 100-106°E). The development of Ch. f. l. salinarius in the freezing littoral of the lake lasts for up to 2 years (half a generation a year), since the larvae remain in an anabiotic state for 8-9 months, frozen into the ice, at an air temperature of -20°C. In Greze's opinion, the other chironomid species (mainly Orthocladiinae) that inhabit the non-freezing part of the lake bottom produce one generation a year.

As we can see from Fig. 1, B, only one emergence of Chironomidae is possible in the waters of the Arctic zone at best, and only the stenothermal-psychrophilic species can produce one generation a year, while the other forms produce one generation in two years. Annual emergences of the latter are possible only if a body of water contains two populations that emerge every spring.

It is not excluded that, at the more northern latitudes, one emergence in two years is also possible with one population present in a body of water.

Unfortunately, we are not aware of any data being published on the number of emergences of Chironomus in the waters of the subarctic zone. All the major data concerning this question have to do with the waters of the temperate climatic zone. Based

on a study of the population dynamics of the larvae of Ch. f. l. semireductus (Streltsov, 1958), the bodies of water near the Arctic Circle, e.g. Syamozero (62°N and 33°02'E) apparently contain one population of the species with one generation and one emergence in spring (Fig. 1, C). The same was observed by K. Dahl (1930) in the Norwegian lakes. According to A.I. Shilova (1960), Ch. plumosus in the coastal zone of the Rybinsk Reservoir up to a depth of 2 m at 58° N lat. has one complete (spring) emergence and one incomplete (summer-autumn) emergence, i.e. a part of the population has two generations, and the other part has 1.5 generations. In another paper, A.I. Shilova (1958) notes two generations (235) in Ch. cingulatus, Ch. dorsalis, Ch. obtusidens and Ch. (Camptochironomus) tentans and one generation in Ch. pilicornis F. in the shallow waters of the reservoir. A little farther south, in the waters of the Moscow area at 55-56° N lat., Ch. plumosus and Ch. tentans at depths of up to 2 m are characterized by two complete emergences (Grandilevskaya-Deksbakh, 1935; Borutsky, 1939; Yablonskaya, 1947; Sokolova, 1962) and two generations (Fig. 1, D).

The number of emergences gradually increases as we move southward, which is unquestionably related to the decrease in the under-the-ice period and to higher summer water temperatures. For example, S.M. Lyakhov (1954) notes that Ch. f. l. semireductus emerges 2-3 times in the ponds of the Kuibyshev Region (53°N lat); Ch. dorsalis and Ch. plumosus emerge three times and Ch. annularius and Ch. heterodentatus four times from the waters around Saratov (51°15' N lat) (Konstantinov, 1952, 1962); according to I.A. Nosova (1952) and S.N. Skadovsky (1952), Ch. f. l. plumosus

and Ch. f. l. semireductus emerge 3-4 times from the ponds around Kamyshin (50°07' N lat); I.K. Vonokov (1950) notes that Ch. f. l. plumosus emerges four (five) times from the ilmens* of the Volga delta (46° N lat); in the ponds at Goryachy Klyuch (Hot Spring) of the Krasnodar Territory (44°40' N lat), A.Ya. Pankratova (1959) noted the same number of emergences in Ch. cingulatus which emerged from the larvae of Ch. f. l. plumosus and Ch. f. l. thummi (Fig. 1, E).

The same is also observed in two eurythermal species, Ch. decorus and Ch. plumosus, on the American continent in the temperate zone. The second species produces one generation in the profundal zone with an emergence in August in the lakes of Saskatchewan (Canada), Lake Ronge according to J.H. Mundie (1959) and Lake Waskesiu according to J.G. Rempel (1936) (located at 55°N lat and 105° W long and at 53° N lat and 106° W long). Much farther south in the deep Lake Pepin in the state of Minnesota, USA (44° N lat and 92° W long), one generation was noted by M.S. Johnson and E. Manger (1930) in the deep part of the lake and two generations in the shallow waters. One generation is also indicated for the other deep lakes of Minnesota, whereas three generations has been noted for this species in the shallow and warm overgrown Cedar Bog lake (45° N lat and 93° W long) (Lindeman, 1942). The same picture is observed in Ch. decorus. In Lake Castello (Ontario, Canada, 45°33' N lat and 78°20' W long), this species emerges once in the littoral zone in June-July (Miller, 1941); it is not observed below the thermocline. Mundie (1959), on the other hand, notes an emergence from Lake Ronge from a depth of 13.5 m in the middle of August.

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*lakes in the Volga delta - transl.

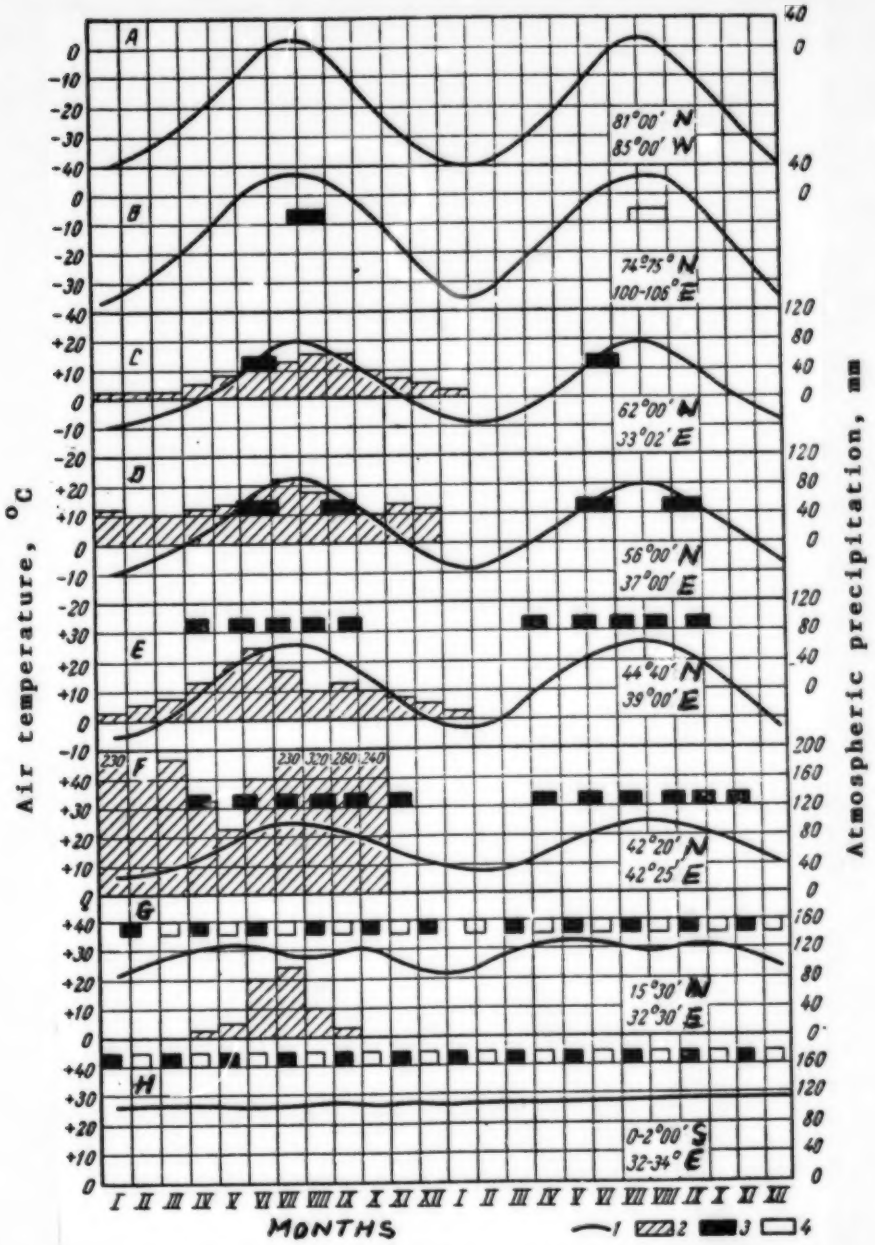

Fig. 1. Number of emergences and generations of eurythermal Chironomus species per year in shallow (up to 2 m) lowland continental water bodies at different geographic latitudes between 30 and 50° E long.

A - Lake Hazen on Ellesmere Is. (Canada); B - Lake Taimyr; C - Syamozero; D - Lake Beloye in Kosino; E - the ponds at Goryachy Klyuch (Krasnodar Territory); F - the ponds at the Dzhapan fish hatchery (western Georgian SSR); G - Nile R. at Khartoum; H - Lake Victoria (Central Africa); 1 - annual variation in air temperature, 2 - annual variation in atmospheric precipitation, 3 - emergence of flies of the genus Chironomus of the first population, 4 - emergence of Chironomus flies of the second population

Farther south in the lakes of Illinois (USA) in the vicinity of Urbana (41°N and 88°W), J.R. Malloch (1915) notes that Ch. decorus clearly emerges twice, in May-June and in September-October. Lindeman (1942) counted three generations in the shallow Cedar Bog lake, and C. Ping (1917) indicated five generations in the vicinity of Ithaca, New York (42°21' N and 75°20' W). The slight difference in the number of emergences and generations should apparently be attributed to the authors' individual approach to determining the number of emergences, as well as to the nature of the water bodies. There is no doubt that the thermal and trophic conditions in a small shallow body of water are more conducive to larval growth than at the same depth in the littoral zone of large deep lakes. In any case, the tendency towards an increase in the number of emergences and generations as we move southward is quite apparent in both species.

Data are available on the ponds of the Dzhapan fish hatchery which is located even farther south in the subtropical climatic zone between 30 and 50° E long. in the vincinity of Samtredi (42°20' N and 42°25' E) in the western part of the Georgian SSR (Ovinnikova et al., 1961). As we can see from Fig. 1 F, the average monthly temperatures in the lowland regions of Western Transcaucasia do not drop below zero, which is more conducive to larval development than in the cis-Caucasus. Here we find that Ch. f. l. plumosus emerges as many as 6-7 times a year, and that two populations are possible. It is interesting to compare these data with those on the Tashkepri Reservoir (36°20'N and 62°40'E) in the Murgab basin. The tabulated data of T.M. Sinyagina (1958) show that

Ch. f. l. semireductus would have emerged the same number of times if it had not been for the substantial annual decrease in the water level of the reservoir. Three emergences have already been noted during the relatively cold spring period (about 8°C in January and about 20°C in May); during the hottest summer and autumn months, the greater part of the bottom dries up and, therefore, contains no larvae.

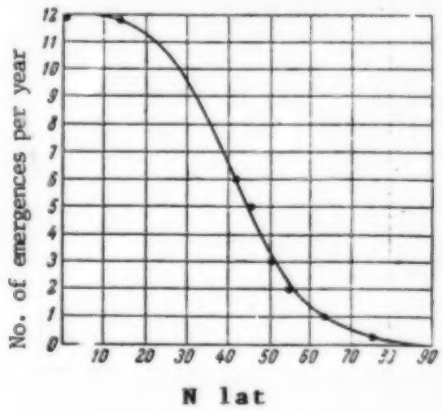

Fig. 2. Curve denoting the number of emergences per year by eurythermal species of the genus Chironomus in lowland continental water bodies from a depth of 2 m at different geographic latitudes between 30 and 50 E long

Data are available only for the Nile in the vicinity of Khartoum (15°30' N and 32°30' E) where water bodies of the tropical climatic zone are concerned. According to D.J. Lewis et al. (1954) and D.J. Lewis (1957), winter is the period of vigorous emergence by Tanytarsus lewisi Freeman, and less vigorous by Procladius sp., Cryptochironomus aegiptinus, Cr. graminicolor, etc. Judging by the curves presented by the authors, distinct monthly peaks are noted in the vigorous emergence of Tanytarsus throughout the winter. There are no emergence data for the rainy summer period, but the higher temperature in summer and the

higher than usual humidity indicate that larval development in summer should proceed at the same rate with monthly emergences. True, these data apply to Tanytarsus, rather than Chironomus, and to river conditions, rather than stagnant water bodies; however, considering that the temperature in stagnant waters is even higher, we are correct in assuming that the eurythermal species of Chironomus, which require about one month for complete development at these temperatures (Derzhavin, 1947; Konstantinov, 1958), also emerge every month (Fig. 1, G). Of these species, Ch. palustris Kieff., Ch. plumosus L., etc. are found in the lakes of tropical Africa.

This assumption has been conclusively proven by Macdonald's investigations (W.W. Macdonald, 1956) in the Central African Lake Victoria (0-2°S lat and 32-34°E long) which is located in the subequatorial climatic zone. This author has conducted a detailed study of the biology of several prolific species of Chironomidae and Culicidae in the northern gulf of the lake. Macdonald has concluded that all of the studied members of these families [Ch. f. l. plumosus, Tanytarsus guttatipennis Goetgh., Procladius umbrosus (Goetgh.), Chaoborus (Neochaoborus) anomalus Edw. and Ch. (Sayomyia) pallidipes Theo. (?)] emerge monthly throughout the year. Since the complete development of the insects from egg to imago takes about 2 months with a constant temperature of 25-26°C at the bottom of the gulf throughout the year, Macdonald believes that there are two populations of each species in the lake, and that their emergences alternate (Fig. 1, H). The periods of their emergence and their swarming are related to the lunar phases.

The emergences take place from the new moon to the half moon, with one peak of emergence on the 2nd-3rd day after the new moon, and the second peak 3-4 days prior to the new moon; emergences and swarmings are not observed during periods of a gibbous moon. (238) A similar phenomenon is also noted for may flies in Central African lakes.

Such are the variations in the number of emergences and generations in the different climatic zones. As we can see from Fig. 2, there is a distinct tendency towards an increase in the number of emergences from the North Pole to the Equator. However, we must remember that these climatic zones fall into a number of climatic regions and subregions characterized by a set of climatic factors (Alisov, 1956) that produce marked differences in the habitat and growth of the larvae found in the same climatic zone. As an example, let us examine the waters of the temperate zone of Eurasia at a latitude of about 50° N, which have been studied to the greatest extent (Fig. 3).

In the western part of Eurasia, the dominant climate is that of the western coasts of the continents, which is characterized by a relatively cool summer, a high humidity and a substantial amount of precipitation throughout the year. In the ponds of central England (51°50' N and 0°10 E), the sum of temperatures according to Mundie (1957) is sufficient for the development of two generations of Ch. plumosus, but the emergences of the insects are dragged out because of a prolonged spring and prolonged autumn (Fig. 3, A).

As we move eastward, away from the Atlantic Ocean, the climate becomes continental, i.e. the summer temperature increases and the winter temperature drops. In the pond-type water bodies of Western Europe, Ch. plumosus also produces two generations, but the emergences are not as prolonged, as we can see from Lellak's data (J. Lellak, 1953, 1953a) for the oxbow lakes along the Labe R. in Czechoslovakia (50°40' N and 15°20' E) (Fig. 3, B).

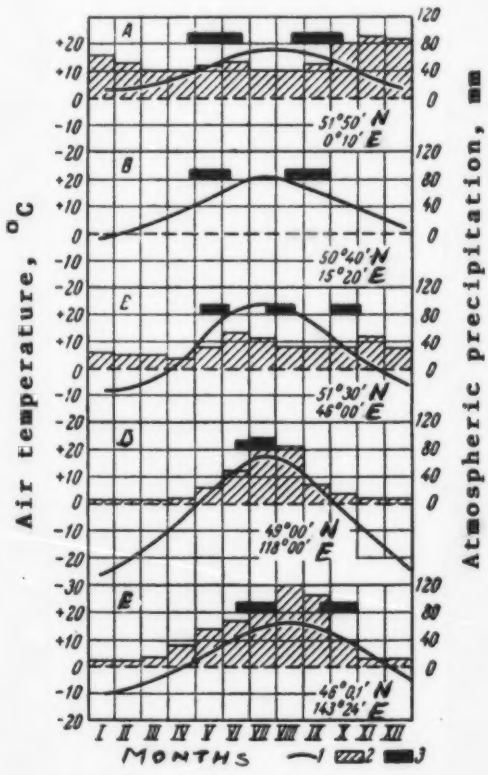

Fig. 3. Number of emergences per year by eurythermal species of the genus Chironomus from water bodies in the temperate zone of Eurasia (up to 2 m deep), located at about 50° N lat

A - a pond in England, B - ponds in Czechoslovakia, C - water bodies in the vicinity of Saratov, D - Lake Dalainor (Chinese People's Republic), E - lakes of Southern Sakhalin (nomenclature as in Fig. 1)

In the vicinity of Saratov (51°30' N and 46°00' E) where the continentality of the climate is more pronounced, Ch. dorsalis and Ch. plumosus emerge three times according to A.S. Konstantinov (1952, 1962); naturally, this is due to the hot summers (Fig. 3, C). In the Aral Sea (43-46° N and 58-61° E) which is located in the zone of a markedly continental climate, Ch. behningi (the larvae of which were regarded as Ch. f. l. plumosus-reductus) is characterized by one vigorous emergence in August-September and by an insignificant emergence in spring (Ye.A. Yablonskaya, 1960). For the waters farther east, we have only A.I. Mikulin's brief information (Mikulin, 1933) on the emergence of flies from the larvae of Ch. f. l. semireductus at the end of July—beginning of August in Lake Balkhash (46°40' N and 73°20'-79°20' E) and Liu Chen-Tsung's data (1960) on their emergence from the larvae of Ch. f. l. plumosus at the end of June in Lake Dalainor in China (49° N and 118° E) (Fig. 3, D). (239)

For the territory of the Far East where the climate of the eastern coasts of the continents predominates, data on the number of emergences of these insects have been provided by A.S. Konstantinov (1950) and T.A. Koreneva (personal communication). The first author provides information about the Chironomidae from Lake Bolon' in the Amur basin (45°40 N and 136°40' E), but since he gives no data on the genus Chironomus, we shall not dwell on his paper; instead, we shall examine T.A. Koreneva's material. This author gives a brief description of the life cycle of Ch. f. l. plumosus in the lakes of Southern Sakhalin (46°00' N and 143°24' E); she indicates only two emergences, the second one from

larvae lagging in their development (Fig. 3, E). This delayed development is attributed to prolonged freeze-up (130-140 days of the year) and low summer temperatures (average temperature for July not higher than 16°C). Ch. f. l. plumosus emerges four times at the same latitude in the vicinity of Astrakhan.

Number of emergences and generations in relation to the depth of a body of water

The complete characteristic depicted in Fig. 2 can be expected only when shallow water bodies or shoal waters (up to 2 m) are compared, and these being at an altitude of 0-200 m, since the temperature conditions in waters of the same climatic zone also depend on the level of a body of water above the sea, its morphology and its distance from the seacoast.

As far as we know, the change in the number of generations of Chironomus in relation to depth was first noted by Johnson and Munger in Lake Pepin (1930). Similar changes were noted by Borutsky (1939) for Lake Beloye in Kosino (near Moscow) (Fig. 4). In this lake, Ch. plumosus produces two generations and emerges twice at a depth of 2 m, and only one generation despite two emergences at a depth of 4 m; in the intermediate zone, we observe a combination of this, partly two and partly one generation, i.e. half a year is required for the development of some larvae of a generation, and a whole year for the development of others. At a depth of 5-7 m, we observe one generation a year; during a meteorologicall unfavorable year and the one following it, we observe one generation in 1½ or 2 years. Not a single generation is found at depths of 9-13 m, since the young larvae of the spring and autumn generations

die off almost completely as a result of unfavorable conditions in the profundal zone (the presence of hydrogen sulfide), while the surviving larvae migrate to the littoral zone. Later on, a number of other authors established a different number of emergences from different depths. For example, one complete emergence of Ch. plumosus in the profundal zone and two emergences (spring and summer) in shoal water have been noted by I.V. Sharonov (1951) in Lake Sevan, by Lellak (1953) in a deep pond in Czechoslovakia, and by A.I. Shilova (1960) in the Rybinsk Reservoir. A decrease in the number of generations with depth is also observed in other species of Chironomidae. For example, Mundie (1957) notes that (240)
the number of emergences from the littoral (2 m) to the profundal zone (7 m) in one of the ponds in England decreases from 2 to 1 in Parachironomus vitiosus Goetgh., from 3 to 2 in Limnochironomus nervosus Getgh., L. pulsus Walk. and Polypedilum nubeculosum Meig., and from 4 to 3 in Tanytarsus lugens Kieff. Data on other species are also available in the literature (Miller, 1941; Lindeman, 1942; Brundin, 1949; Sokolova and Koreneva, 1959, etc.). These far from exhaustive data indicate without a doubt that the number of emergences depends on the temperature, trophic and oxygen conditions at the bottom of a body of water at different depths in the temperate climatic zone. What is the situation in the waters of other climatic zones?

In deep tropical bodies of water, the temperature of the water is high not only at the surface, but at the bottom as well; for example, the water temperature in the Central African Lake Nyasa (10-14° S lat) in December is 27.5-29.7°C at the surface, and

22.75°C at a depth of 193 m (Zernov, 1949); the fluctuations in temperature are even smaller in Lake Victoria which is located on the equator. Under such temperature conditions, one would expect Chironomus to emerge monthly from all the depths in tropical lakes if, of course, they are populated by larvae. Development is slower only at very large depths where the temperature drops to 23°C in winter; consequently, there may be fewer emergences.

The opposite is observed in deep polar waters. Unlike tropical waters, they are characterized by the presence of an ice cover for a long period of time, during which the temperature drops; during certain years, the ice does not melt at all. As in the tropics, the annual fluctuations in temperature are insignificant; shoal waters are a less favorable habitat, since they freeze to the bottom. Whereas Chironomus are expected to emerge monthly from practically all depths in tropical waters, they emerge only once from all depths in arctic and antarctic waters, and they are not found at all in high-polar waters.

An altogether different picture is observed in the waters of the subarctic, temperate and subtropical zones. These waters undergo greater fluctuations in temperature as compared with arctic and tropical waters. Vertically, the temperature decreases considerably towards the bottom, but usually unevenly, forming a thermocline. At depths of over 30 m, the temperature of the waters in the temperate zone stays at about 4-5°C throughout the year. The temperature characteristics of a body of water determine the annual temperature variation in the near-bottom layers at different depths, which in turn affects the growth rate of

Chironomus larvae at these depths and, consequently, the emergence of the flies. Proceeding from the temperature characteristics of the deep waters of these climatic zones, we can easily see that the pattern and nature of the emergences of eurythermal Chironomus will change as we move from the equator towards the poles. The number of emergences in shoal waters decreases naturally from 12 to 0 (as shown in Fig. 2), depending on the geographic and climatic location of the body of water. However, the number of emergences and generations will also decrease from the littoral to the profundal zone. In waters without a thermocline, we observe a gradual decrease in the number of emergences and generations from the maximum number in shoal water (for the given latitude and longitude) to 0, as we have established for Lake Beloye (Fig. 4). The picture is more complex in waters with a more sharply defined summer stratification. A gradual decrease in the number of emergences is observed from the epilimnion, followed by a sharp decrease (usually to one emergence) below the thermocline, and the total absence of emergences from depths with a constant low temperature of 4-5°C. Examples of this are given by Miller (1941) for Lake Castello in Canada, and by I.V. Sharonov (1951) for Lake Sevan in Armenia.

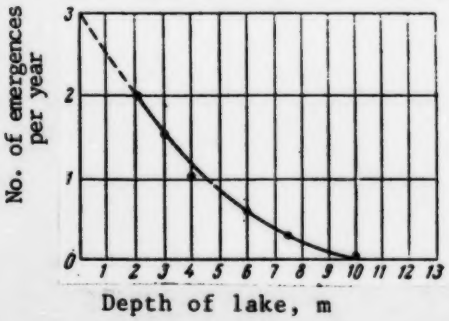

Fig. 4. Curve depicting the number of emergences of Chironomus plumosus a year from different depths in Lake Beloye near Kosino during 1935-1936

(241)

However, we should mention that complete consistency in the number of emergences is possible only when the entire bottom of a body of water is colonized by some eurythermal species of Chironomus, which does not usually occur. This is possible in eutrophic bodies of water where the bottom substrate is more or less uniform throughout. Usually, one species keeps to the littoral or sublittoral zone, while the profundal zone, specifically the hypolimnion, is populated by another species (usually Ch. anthracinus in European waters) which emerges only once, in spring, from all the depths regardless of the geographic location of the body of water (Thienemann, 1951; Sharonov, 1951; Johasson, 1954; Mundie, 1957; Sokolova and Koreneva, 1959, etc.).

Number of emergences and generations in relation to the altitude of a body of water above sea level

The eurythermal species of Chironomus ascend high into the mountains. In the Transcaucasus, for example, Ch. f.l. semireductus is common in the waters of the Georgian and Armenian SSR, located at an altitude of 2000 m above sea level and higher. According to S.G. Lepneva (1950), the larvae of Ch. f.l. plumosus dominate in the Azerbaijanian lakes Gek-gel and Khanly-gel; the latter is located at an altitude of 3017 m, and is surrounded by snow for 8 months of the year. The larvae of Ch. f.l. plumosus inhabit marginal alpine lakes (Thienemann, 1954). There is no doubt that the number of generations and emergences of the eurythermal species of Chironomus also varies with the altitude of a body of water above sea level. Unfortunately, only several papers are available on the life cycles of Chironomus in alpine bodies of water.

According to I.V. Sharonov (1951), Lake Sevan is inhabited by three species of Chironomus, i. e. Ch. plumosus, Ch. anthracinus (=Ch. f. l. thummi in A.I. Sharonov) and Ch. tentans. The lake is located in the subtropical zone at an altitude of 1914 m (40°40' N lat and 45°00'-45°30' E long), but despite this, Ch. plumosus emerges only twice in the littoral zone and once in the profundal zone, whereas the same species emerges 6-7 times a year in the lowland ponds of the western Georgian SSR. According to B.P. Alisov (1956), the climatic conditions of Lake Sevan are reminiscent of those in the waters of the central regions of the European part of the USSR, and because of this, the number of emergences by Ch. plumosus is the same as in the waters around Moscow, and the number of emergences by Ch. tentans is the same as in the Rybinsk Reservoir (2 emergences). A similar picture is observed in the bodies of water in the vicinity of Ithaca, New York, USA. Ch. tentans also produces two generations here (Sadler, 1935), though the given bodies of water are located 16° farther south in comparison with the Rybinsk Reservoir. This should be attributed to the colder climate of North America as compared with Eastern Europe, and to the higher altitude of the bodies of water around Ithaca (500-1000 m), which together are less conducive to larval development. As in other lakes, Ch. anthracinus produces one generation in Lake Sevan. We have already discussed the number of emergences of Chironomidae in Lake Victoria (Central Africa). Here we shall mention only that the lake is located at an altitude of 1134 m above sea level, and that Ch. plumosus emerges from it 12 times.

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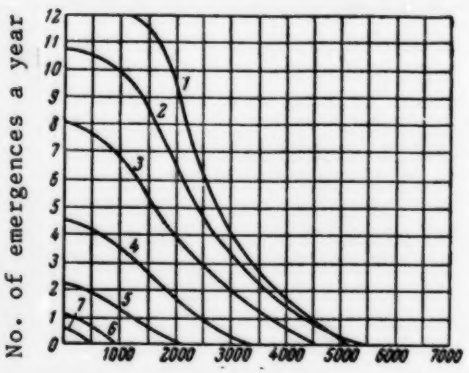

Fig. 5. Curves denoting the number of emergences of eurythermal Chironomus species from depths of up to 2 m in continental bodies of water located at different altitudes above sea level in various climatic zones of the northern hemisphere

1 - 0-20°, 2 - 20-30°, 3 - 30-40°, 4 - 40-50°, 5 - 50-60°, 6 - 60-70°, 7 - 70-80° N lat

On the basis of climatological data, one can assume that the number of generations of eurythermal species in the equatorial, subequatorial and to some extent tropical climatic zones will diminish with the altitude above sea level, but not as sharply as in the other climatic zones. The effect of the relief on climate in these zones is expressed mainly by a general decrease in air temperature with altitude (by an average 0.5° every 100 m) and by related changes in other elements. For example, the temperature at an altitude of 2850 m in the Andes (South America) in the vicinity of Quito (0°12' S lat and 78°30' W long) is 15°C, with the amplitude of annual variations equal to about 1°; on the other hand, the constant annual temperature at sea level is about 26°C. It is evident from this that the insects will emerge 12 times in shallow bodies of water at the foot of mountains, whereas in alpine bodies of water, even though the insects emerge all year round due to a stable temperature, the number of emergences will decrease,

for the lower temperature will slow the growth rate of the larvae. There should be no emergence at all at an altitude of a year-round 0° isotherm. The 0° isotherm lies at an altitude of 4900-5000 m at the equator in the Andes, South America. Naturally, there are no Chironomus larvae in bodies of water at these altitudes. In Lake Victoria, which is located on an alpine plateau, a temperature of 25-26°C holds out even at an altitude of over 1000 m, and, according to Macdonald (1956), monthly emergences are even observed here.

As we move from the tropics towards the poles, the number of emergences of Chironomus in alpine bodies of water is determined by the latitudinal and longitudinal position of the body of water on the one hand, and by the altitude of the snow line and, finally, by the amount of heat available during the ice-free period, which determines the number of generations developing at a given depth. Proceeding from the data on the number of emergences and generations at depths of up to 2 m in lowland bodies of water (see Fig.2) and the data on the altitude of the snow line in mountain systems (Alisov et al., 1952, p. 201) at different latitudes of the northern hemisphere, we can plot a graph (fig. 5) in which the curves depict the number of emergences of eurythermal Chironomus species from depths of up to 2 m in bodies of water located at different altitudes above sea level in different climatic zones of the northern hemisphere. We should keep in mind that this graph depicts the general tendency, and the values may vary somewhat in each specifice case due both to the differences in the climatic conditions at the same latitude but at different longitudes, and to the

differences in the altitude of the snow line not only in the mountain systems located at different longitudes, but even in the same mountain system (e.g. the northern and southern slopes on the seaward and landward sides of the continent, etc.). It goes without saying that the number of emergences in deep alpine bodies of water will also decrease from the littoral to the profundal zone, which is observed, for example, in Lake Sevan.

Emergences of Chironomidae as a factor of the food consumed in a body of water by fish and the food supply of the latter

The food supply of the fish in a body of water is determined by the annual production of food organisms; the food consumed in a body of water by fish and the food supply of the latter are determined largely by the availability of this or that food organism to the fish. The food supply may be very abundant as to the numbers and biomass of food organisms and their annual production, but the food consumed by the fish may constitute a small quantity because of its inaccessibility to the fish. The food consumed in a body of water by fish and the food supply of the latter may also diminish considerably because of the complex system of food interrelations in each body of water (Borutsky, 1959, 1961). (243)

This applies most of all to the Chironomidae, the larvae of which live in the bottom substrate or mine aquatic plants, and therefore are not very accessible to fish. The high degree of protection enjoyed by the larvae has been demonstrated quite well in laboratory experiments by S.V. Suetova (1937, 1939, 1951), field experiments by A.V. Assman (1960) and in first-hand observations

in bodies of water. A good example of the latter is the nonutilization of the abundant food supply of the abyssal zone of Lake Sartlan (Pirozhnikov, 1929) and the Aral Sea (Berwald, 1961) by the bream, or the nonutilization of the abundant supply of Ch. plumosus in the ponds of the Volgograd Region by the crucian carp (Nosova, 1952). In the bodies of water where the abundant supply of midge larvae is almost completely inaccessible, the period of emergence of the flies is almost the only time when commercial bottom-feeding fish can utilize them. At this time, both bottom-feeding, plankton-eating and even carnivorous fishes begin to feed on pupating larvae and pupae.

The period of emergence of Chironomidae is widely used for supplementary feeding by the fish population in each body of water of all the climatic zones. For example, I.I. Greze (1953 a) indicates that the Ob whitefish, broad whitefish and arctic grayling of Lake Taimyr consume the pupae and imagines of chironomids and other insects in addition to benthic organisms; according to Dahl (1930), the pupae and imagines of Ch. plumosus in the lakes of Norway are utilized by the loach in spring and summer; according to our own data (Borutsky, 1939), of the total annual production of Ch. plumosus consumed by fish in Lake Beloye near Kosino, approximately 70% consists of pupae which during spring emergence are voraciously consumed by the common perch; a high percentage of pupae has been noted in the stomachs of the American yellow perch from the lakes of Wisconsin (USA) by A.S. Pearse and H. Achtenberg (1920); according to Ye.A. Yablonskaya (1960a), almost the entire fish population in the Aral Sea (mainly the Aral

white-eye, the Aral shemaya and sabrefish) feed on the larvae and imagines of Ch. behningi during its emergence; Lewis (1957) indicated that, during the emergence of chironomids on the Nile, the pupae of Tanytarsus are consumed by Micralestes acutidens Peters, and the pupae of Nilodorus brevibucca Kieff. by Chelaethiops bibie (Johannes) and other members of the ichthyofauna of the Nile. According to Macdonald (1956), the chironomid larvae and pupae in Lake Victoria (Central Africa) are found in greatest abundance in the intestines of Mormyrus kannume Forsk. during the periods of emergence. We can give a number of other examples confirming the extensive use of chironomid pupae by fish in bodies of water of different geographic latitudes.

However, we must remember that highly complex interrelations exist between the Chironomidae and the fish population that feeds on them; they consist of a system of adaptations of the food organisms for protection against the fish, and of the fish population for better utilization of the Chironomidae.

As demonstrated by a number of investigations (Borutsky, 1939; Miller, 1941; Scott and Opdyke, 1941; Mundie, 1957, 1959; Palmen, 1955, 1958; Lewis, 1957; Morgan, 1958; Lindeberg, 1958; Tjönneland, 1958; Chernyshev, 1961, etc.), the Chironomidae in all the more or less deep bodies of water (stagnant and running) usually emerge during the dark hours with peaks after sunset and before sunrise (in faint light). Emergences during the daytime are observed in deep bodies of water, usually either in gloomy weather, or during the autumn in cold weather and faint light, or during solar eclipses. Bottom-feeding fish, particularly those feeding on

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Chironomidae, forage mainly during the dark hours as well. This is quite natural, since the larvae that rise to the surface of the substrate prior to pupation and the pupae in the water as they rise to the surface of the water become more accessible (Borutsky, 1935, 1939; Nikolsky, 1940). It is interesting to note that twilight and nocturnal emergences are observed only during warm spring and summer weather when the fish forage; in autumn, when the intensity of feeding diminishes, the insects emerge at the same rate throughout the 24 hours of the day.

There is no doubt that the time of emergence is of adaptive significance, for the pupae are less noticeable in the water at dusk and at night, just as the emergence of the insects in the tropics is confined to the dark periods of the month (new moon). The survival of the species is also ensured by the brief pupation of the larvae, the rapid ascent of the pupae to the surface of the water and the almost instantaneous emergence of the flies from the pupae. The emergence is usually quick, simultaneous and abundant, which prevents them from being consumed en masse by the fish; it follows from this that prolonged emergences of chironomids should increase the food consumed in a body of water by fish and the food supply of the latter to a greater extent than quick and simultaneous emergences.

We would like to mention another two points indicated in the literature. These are the round-the-clock emergences from shallow pond-type bodies of water on the coast of the Gulf of Finland (Lindeberg, 1958) in summer and the emergences on Lake Taimyr through hydrological holes in early spring long before the lake

is freed of ice (Greze, 1953). The round-the-clock emergences in the first case are apparently due to the absence of a fish population in the ponds, while the emergences from the ice holes in the Arctic should apparently be regarded as an adaptation to produce an annual generation; the latter is corroborated by I.I. Kurenkov's personal communication that the fish in Kamchatka waters in winter feed on the pupae and even flies of Orthocladiinae, which indicates that these insects pupate and even emerge under the ice.

However, despite these adaptations of the pupae to evade the fish preying on them, we can say with certainty that the emergences of the Chironomidae and particularly the species of the genus Chironomus increase the amount of food consumed in a body of water by fish and the food supply of the latter. The more emergences per year and the longer they last, the more accessible food becomes to the fish. The number of emergences and generations of eurythermal Chironomus species increases consistently from the poles to the equator, from the summits of mountain systems to the lowlands at the foot of the mountains, and from the depths to the shallows. Consequently, the highest productivity of eurythermal Chironomus species and other chironomids and the highest production of benthophages can be expected in shallow lowland equatorial and tropical bodies of water.

Without dwelling on the literature dealing with the natural fish productivity of inland bodies of water in different climatic zones, we shall but mention the paper by B. Vibert and K.E. Lagler (1961), where it is stated that small tropical bodies of water such as Lake Chad and Africa or Lake Tople-Sap in Cambodia are the world's most productive natural bodies of water.

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EMERGENCE OF CHIRONOMIDAE (DIPTERA) IMAGINES FROM CONTINENTAL WATERBODIES OF DIFFERENT CLIMATIC BELTS AS A FACTOR OF FOOD SUPPLY OF FISHES

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Summary

The number of emergences of eurythermal species belonging to the genus Chironomus in shallow waterbodies (less than 2 *m* depth) in localities the altitude of which is not higher than 200 *m* above sea level reguralry decreases from 12 to 0 in directions from the equator towards the poles. There are two Chironomus populations with alternating time of imagines emergence in tropical and arctic waterbodies, while in those of intermediate climatic belts there is, as a rule, one population only (figs. 1 and 2). Both the quantity and the character of the imagines emergences undergo changes in one and the same climatic belt in relation to the longitude at which the waterbody is situated (fig. 3). In the waterbodies of the moderate climate, without thermocline, a gradual decrease of the number of emergences is observed from the maximal in shallow sites (for the given latitude and longitude) down to 0 in the profundal ones (fig. 4). The pattern is more complicated in the waterbodies with a distinct thermocline. The number of imagines emergences depends upon the situation of the waterbody above sea level; in mountain waterbodies in the direction from the equator towards the poles this number is determined by the position of the waterbody with respect to longitude and latitude, and by the height of the snow line as well (fig. 5). The period of imago emergence for eurythermal species of the genus Chironomus is of a great importance for the supply of food for fishes in the waterbodies in all the climatic belts; this role diminishes from the equator towards the poles, and from the foothills to the summits.